Ecological Studies of Carrion Beetles in Hutcheson Memorial Forest

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Abstract: Carrion-baited ground cans were used to collect carrion beetles during the summers of 1961 through 1965. Fresh chicken legs were used as bait and were left in the cans for two-week periods of time. Practically all of the flesh was eaten or decomposed by the end of this period. All collected beetles were identified to family, all Silphidae to species, and all Leptodiridae to genus or species. The members of the Silphidae, Leptodiridae, Histeridae, and Staphylinidae were consistently attracted to carrion and accounted for the bulk of the beetles that were trapped. The Silphidae was the dominant family and the seven species collected accounted for almost half of all the beetles collected. The numbers of individuals of this family were maintained at about the same level throughout the seasonal periods of study in 1961 and 1963. There was no apparent succession of Silphidae species on carrion during the period of time required for total decomposition. The carrion seemed to be most attractive to these beetles from the fifth to the tenth days when it was in the fresh-bloated, bloated, and decay stages. There was a seasonal pattern of change in dominant populations of Silphidae during the six-week summer periods of study. Silpha noveboracensis, the dominant species of early summer, decreased steadily and virtually disappeared by middle summer. Nicrophorus sp., on the other hand, was present in small numbers in early summer but increased steadily and became the dominant species in middle summer. Silpha noveboracensis was the dominant species in three shrub areas during early summer. It was most abundant in the Maple-leaved Viburnum shrub area.

INTRODUCTION

Many beetles are attracted to carrion and one family in particular, the Silphidae, are commonly called carrion beetles. This family of beetles contains some fairly large, brightly colored individuals which have been made famous through the writings of Jean Henri Fabre (1899). Much is known about these beetles, yet more is to be learned. It has been my hope to contribute to this information. This study was conducted in The William L. Hutcheson Memorial Forest, near East Millstone, in Somerset County, New Jersey.

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SHUBECK: CARRION BEETLES

Several studies dealing with various aspects of carrion decomposition and the arthropods associated with it have appeared during the last three or four decades. Payne (1965) conducted a summer study in South Carolina using baby pigs for carrion. He found that insect-free carrion decomposed very slowly and retained its form for many months. Carrion exposed to insects, however, was completely eaten within six days. As a result of this study, the Oak Ridge National Laboratory published a complete list of animal species associated with pig carrion (Payne and Crossley, 1966).

Walker (1957) studied the arthropods associated with decaying fish, cantaloupe and corn meal in four habitats in Tennessee. The differences in species collected, he noted, were due to the courses of carrion decay within the habitats, which in turn were caused by differences in microclimate.

Reed (1958) studied the animal communities associated with dog carcasses in Tennessee. He used paired carcasses, in wooded and pasture areas. The insect populations were found to be smaller in the pasture but succession was faster as a result of the greater heat. Reed also listed the earliest and last days for insect species collected during the course of a full year.

Bornemissza (1957) studied arthropod succession on carrion in Australia along with the effect of carrion decomposition on soil fauna. He found that the various stages of decomposition affected the soil below the carrion differently. This effect persisted, at least to some extent, for over a year.

Fuller (1934) also studied insect inhabitants of carrion in Australia. Although Fuller's efforts were concentrated on blowflies, her paper included some general discussion on Coleoptera. She made note of the great destruction of blowfly eggs and larvae by beetles, ants, and earwigs.

Howden (1950) studied the succession of beetles on carrion in North Carolina and Maryland. She found 14 families of beetles on carrion. One-half of the species present were primarily predators of fly larva and pupa, whereas the other half were necrophagous or of uncertain food habits. The typical succession, as she found it, started with oviposition by flies, followed by invasion of Staphylinidae and Histeridae, and finally the arrival of Silphidae and a number of other families associated with them.

In a previous paper (Shubeck, 1968) I discussed the results of orientation studies. However, this present paper contains the results of studies directed toward three objectives: A survey of beetles associated with carrion; the succession of the families of beetles and the species of the Silphidae on carrion; and the succession of carrion beetles in three different shrub areas within the oak-hickory climax forest.

METHODS

The observations here reported were made between July 1 and August 15 during the summers of 1961 through 1965. The beetles were trapped in gallon

cans buried with the open end flush with the surface of the soil (Shubeck, 1968). Each of the traps was baited with an uncooked chicken leg or "drum stick."

Most collections were made between 2:00 and 4:00 o'clock in the afternoon. The beetles present in the traps on collecting days were removed with large forceps and placed in small jars containing 75% alcohol. Thus, all collections made over the five year period have been preserved. The jars were labeled so that the collecting day, the location, and the individual trap were recorded when the beetles were identified. All beetles were identified to their family designation, all Silphidae were identified to species, and all members of Leptodiridae to genus and, when possible, to species using references by Arnett (1963), Dillon and Dillon (1961), and Lutz (1918). A series of identified specimens have been deposited at the Department of Entomology Museum of the College of Agriculture and Environmental Science, Rutgers—The State University.

The study designed to compare succession by families of beetles and by species of family Silphidae was conducted during the summers of 1961 and 1963. A station was set up in the Maple-leaved Viburnum (Viburnum acerifolium) shrub area of Hutcheson Memorial Forest. Twelve ground cans were arranged in a circle so that each can was ten feet away from each neighboring can (Walker, 1957). The baiting of the cans was arranged so that there were three replicates, each containing a series of baits. The first can contained a chicken leg, the second can a fresh, peeled potato, the third can corn meal, and the fourth can was left empty. Although I had originally planned to look into the succession of insects on corn meal and potato, so few insects were attracted to these baits that they, along with the empty cans, served as controls to the carrion-baited trapping-cans.

Freshly baited traps were set up in two-week cycles. In this way the chicken legs went through cycles of decomposition until little flesh was left. For the sake of convenience, since I collected in three two-week cycles, "seasonal" labels were given to these periods of time; Early summer, July 1 to July 15; Early-middle summer, July 16 to July 31; Middle summer, August 1 to August 15. These dates varied only slightly in 1961 and 1963 since a given cycle always started on a Saturday with the setting of the traps. Collecting trips were made on Tuesdays, Thursdays, and Saturdays, so that for each cycle insects were collected on the 3rd, 5th, 7th, 10th, 12th, and 14th days after the baits had been set. During the 1963 study a record was kept of the condition and approximate degree of decomposition of the carrion on each collecting day.

In 1962 only one cycle was run but it was set up in three distinct shrub layers some distance apart from each other. The Maple-leaved Viburnum station was the same one used in the 1961 and 1963 study. A second station was set up in an Arrowwood-Greenbrier (Viburnum dentatum-Smilax rotundifolia) shrub area which was about 250 meters W.S.W. of Station 1. The third station was set up in a Black-haw (Viburnum prunifolium) shrub area and

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was about 200 meters N.W. of Station 1. This experiment was designed to see if there was any difference in carrion beetle species or succession in relation to different shrub areas within a given forest. Two one-gallon cans were left on the ground at each of the three stations to measure rainfall, and the temperature was recorded on the soil surface at each of the three stations during the collecting trips.

RESULTS

TAXONOMY. Four families of Coleoptera were consistently attracted to the carrion-baited ground cans. They are: Silphidae, the Carrion Beetles; Leptodiridae, the Small Carrion Beetles; Histeridae, the Hister Beetles; Staphylinidae, the Rove Beetles. These families made up the bulk of the Coleoptera collected. In 1961 they accounted for 97% of all beetles taken and in 1963 they accounted for 89% of all beetles collected; they are very important members of the carrion community.

Two genera and seven species of Silphidae were present, Silpha americana, S. noveboracensis, S. surinamensis, S. inaequalis, Nicrophorus orbicollis, N. pustulatus, and N. tomentosus. Tables 1 through 3 show that four of these species, S. americana, S. noveboracensis, N. orbicollis, and N. tomentosus, were collected in modest to abundant numbers, and for convenience I referred to these as the "common" species. On the other hand, Silpha surinamensis, S. inaequalis and N. pustulatus were collected in very low numbers, and for convenience I referred to these as "rare" species.

succession. In terms of this study, succession might be defined as the predictable, sequential appearance and relative abundance of carrion beetle species on a chicken leg during a two-week cycle of decomposition. The presence and abundance of individuals of the families Silphidae, Staphylinidae, Histeridae, and Leptodiridae during six-week periods of observations is recorded in Table 1 (1961) and Table 3 (1963). The Silphidae were the most abundant in terms of numbers of individuals and comprised 46.51% of the four families during 1961 and 1963 (Table 4). The numbers built up to a peak on the fifth to seventh days of each cycle and dropped off to zero by the 12th to 14th days. The numbers of individuals in this family were maintained at about the same level throughout the six-week period of time (Table 4 and Fig. 1).

The numbers of Staphylinidae usually exhibited peaks at about the same time as the Silphidae although their numbers were much lower (Tables 1 and 3). The numbers of Histeridae and Leptodiridae did not describe a definite pattern.

EARLY SUMMER. Silpha noveboracensis was the most abundant species present at this time and an acute peak was present on the fifth day of the cycle in 1961 and 1963. A second, smaller peak was present on the tenth day in 1961. A total of 200 individuals was collected during the early summer cycle in 1961 and 1963 (Table 5).

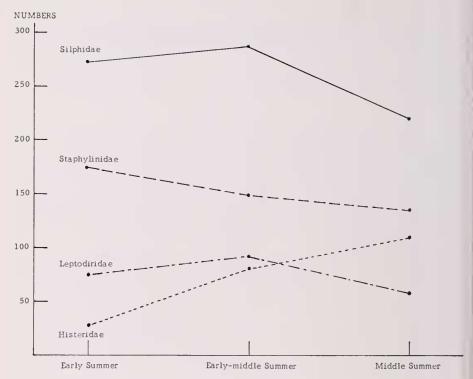


Fig. 1. Total numbers of four families recorded by season in 1961 and 1963.

The number of *Nicrophorus* sp. present during this cycle was only about 25% of the above species and it also manifested a peak, although a modest one, on the fifth day. I found it practical when examining and discussing results of these studies to combine the numbers of *Nicrophorus orbicollis* and *tomentosus* and to refer to these individuals in terms of one taxon, *Nicrophorus* species.

Few individuals of *Silpha americana* were present during this cycle (Table 5) although one or two appeared on several collecting days (Tables 1 and 3).

Prionochaeta opaca (Leptodiridae) was present in small numbers from the third day. In 1961 this species increased to 19 individuals on the seventh day when the other species dropped off considerably for some unexplainable reason (Table 1). In 1963 this species increased in numbers during the second week when the other species were no longer present (Table 3).

EARLY-MIDDLE SUMMER. The numbers of *Silpha noveboracensis* dropped to about 25% of the early summer level (Table 5). There was but one peak at this time and it fell on the fifth or seventh days (Tables 1 and 3).

Nicrophorus sp. showed a two-fold increase in numbers over the early summer period (Table 5), and a modest peak was again evident but it was present on the seventh and not on the fifth day.

Table 1. Carrion beetles collected in 1961.

			Ea1 7/1	rly S /61–	Early Summer 7/1/61-7/15/61	ner /61			山	Early-middle Summer 7/15/61-7/29/61	rly-middle Sumr 7/15/61-7/29/61	dle 5	9/61	ner			Mi 7/2	ddle 9/61	Sun -8/1	Middle Summer 7/29/61-8/12/61		S
Days	3	ıν	7	10	7 10 12 14	14	Total	3	w	7	7 10 12 14	12	14	Total	8	w	7	10	12	10 12 14	Total	Total
Silphidae Silphia americana	-	-		~	-	1	9	-	77	22	ox	Ξ		98			,	,		,	4	90
S. noveboracensis	20	46	13	26		1	106		17	7	۱ د	1 1	1	25	1 1	1	, -	1 1	1 3	1 1	+	132
S. surinamensis	1	-1	-1	1	-1	1	1	1	1	1	1	i	1	1	1	1	1	1	1	-1	1	1
S. inaequalis	1	1	_	2	2	1	w	1	1	1	1	-1	1	1	1	1	1	1	-1	1	1	v
Nicrophorus orbicollis	w	4	4	4	1	S	22	2	10	16	3	12	1	43	-1	42	56	18	-	1	117	182
N. pustulatus	1	1	1	1	1	1	I	1	1	_	1	-	1	2	1	1	-	1	1	-1	_	3
N. tomentosus	Т	7	Т	4	1	7	15	1	N	S	∞	2	1	21	1	-	3	1	1	1	4	40
Leptodiridae																						
Prionochaeta opaca	2	3	19	1	1	1	24	1	I	7	1	1	1	2	I	1	1	-	}	1	1	27
Catops spp.	1	1	3	-	19	1	23	1	1	1	T	1	I	I	1	_	-	1	1	I	2	25
Staphylinidae	12	20	26	11	16	4	68	3	25	19	7	1	1	61	-	12	11	00	6	1	41	191
Histeridae	1	-	2	es	2	-1	6	1	9	3	w	7	-1	16	1	1	1	9		- 1	7	32

TABLE 2. Carrion beetle species collected in 1962.

į		Маг	sk-le	aved	leaved Viba Shrub Area	Maple-leaved Viburnum Shrub Area	Œ		Ar	rowy	Arrowwood-Greenbrier Shrub Area	-Gre	rnbri	10			- x	slack hrub	Black-haw Shrub Area	_ n	
			Ean 6/30	ly S	Early Summer 6/30/62-7/14/62	ner /62		1		Ear 6/30	Early Summer 6/30/62-7/14/62	umm 7/14	ler /62		3		Earl 6/30	:ly S	Early Summer 5/30/62-7/14/62	ner /62	
Days	~	w	1	10	7 10 12 14	14	Total	\m	w	7	7 10 12 14	17	7	Total	3	w	7	01	7 10 12 14	4	Total
Silphidae Silphu americana S. noveboracensis S. surinomensis S. inaequalis Nicrophorus orbicollis N, pustulatus N, tomentosus	24 24 1 1 1 2 4 2 4 2 4 2 4 2 4 2 4 2 4	$=\frac{4}{\kappa}+1$ κ $+$ κ	21 21 1	26	1 1 1 1 1 0	1 - 1 1 1 1 4	2 123 1 1 1 16	[∞]]	20 1 1 1 1 6 9	1 6 1 1 7 1 8	83.2 2.2 2.10	9 22 7 1 1 1 1 6 6 6	0 m =	26 147 147 1 1 25 25	- w m m	1 2 1 1 2 1	8 1 1 8 1 2	7 7 1 1 4 1 11	r & -	12 - 2	165 165 19 19
Leptodiridae Prionochaeta opaca Catops spp.	- %	1 %	1 2	1 -	10	3 10	7 29	2 1	7 9	71	7 2	۱ ~	2 4	23	- 1	- 1	m 1	14	1 1	7 7	29

TABLE 3. Carrion beetles collected in 1963.

			Ea 7/6	rly 5 /63-	Early Summer 7/6/63-7/20/63	ner //63			Ea	rly-r 7/20	Early-middle Sum: 7/20/63-8/3/63	le Su -8/3/	Summer /3/63	Te.			Mic 8/3	Middle Summer 8/3/63-8/17/63	Sum 8/17	ner /63		Summer
Days	8	w	7	10	10 12	14	Total	3	w	~	10	12	41	Total	8	w	~	10	12	14	Total	Total
Silphidae Silpha americana	-	-	1	- 1	- 1	1	2	4	12	9	7	Ī	- 1	24	1	8	24	3	1	4	30	56
S. noveboracensis	w	92	13	I	I	T	94	7	I	14	7	ı	1	18	I	7 -	×	ı	1	1	2 -	122
S. surinamensis	1 1	1 1	1 1		1 1		1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1	⊣ 1	1 1	1 1	1 1	1 1	٦ ١	⊣ 1
Nicrophorus orbicollis	- 1	- 1	- 1	- 1	- 1	-1	1	-1	_	18	3	2	1	24	7	1	15	3	-	3	29	53
N. pustulatus	1	1	-	1	1	I	-	1	1	1	1	1	1	2	1	7	1	1	ı	ı	2	w
N. tomentosus	-1	1	-	1	1	1	1	1	1	6	1	1	1	6	-	I	12	3	~	I	19	50
Nicrophorus sp.	9	14	1	I	1	1	20	16	17	1	I	1	I	33	I	4	I	I	1	ī	4	22
Leptodiridae																						
Prionochaeta opaca	2	1	-	3	7	7	20	∞	2	2	4	30	39	82	1 .	1	∞ ;	ı	(~)	4 ,	19	124
Catops spp.	3	1	1	7	7	-	∞	w	1	!	I	1	_	0	4	10	10	ı	n	٥	55	49
Staphylinidae	15	26	23	13	ıv	3	82	46	22	6	4	3	4	88	18	24	13	26	w	9	92	265
Histeridae	2	11	- 1	1	3	2	19	12	36	Ξ	3	-	-	64	12	30	22	22	-	15	102	185

Table 4. Changes in total numbers of important beetles by season, during 1961 and 1963, and percentages of major families for entire season, 1961 and 1963.

Families	Early Summer	Early- middle Summer	Middle Summer	Totals	%
Silphidae	272	287	222	781	46.51
Leptodiridae	75	93	57	225	13.40
Staphylinidae	174	149	133	456	27.15
Histeridae	28	80	109	217	12.92
Totals	549	609	521	1,679	99.98

Silpha americana was now found in much larger numbers and there was a definite peak on the fifth day of the cycle.

Prionochaeta opaca barely made its appearance during this season in 1961. In 1963 it was present in very small numbers during the first ten days and then increased very sharply on the 12th and 14th days when the other species all but disappeared.

MIDDLE SUMMER. The number of *Silpha noveboracensis* was now insignificant (Table 5 and Fig. 2). In 1961 one individual was taken on the seventh day of the cycle (Table 1). In 1963 two individuals were taken on the fifth day, eight on the seventh day and none thereafter (Table 3).

Nicrophorus sp. was now the dominant carrion beetle (Table 5 and Fig. 2). A peak of 59 individuals was reached on the seventh day in 1961 (Table 1). In 1963 a peak of 27 individuals was present on the same day of the cycle (Table 3).

Silpha americana was present in very small numbers on the seventh and tenth day of the cycle in 1961. In 1963 this species was present on days five, seven and ten with a conspicuous peak on the seventh day.

Prionochaeta opaca was barely present during this season in 1961. In 1963 it was present in larger numbers and once again was quite conspicuous during the second week of the cycle when the other species had all but disappeared (Table 3).

TABLE 5. Total numbers of species recorded by season in 1961 and 1963.

	Early Summer	Early- middle Summer	Middle Summer	Totals
Silpha americana	8	110	34	152
S. noveboracensis	200	43	11	254
Nicrophorus sp.	58	130	173	361
Opaca prionochaeta	44	87	20	151
Totals	310	370	238	918

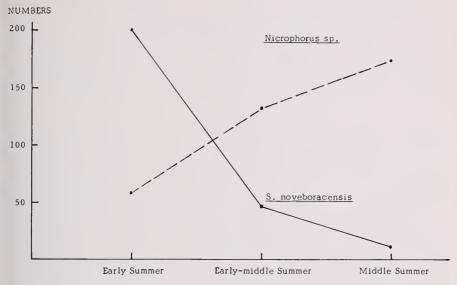


Fig. 2. Total numbers of two species recorded by season in 1961 and 1963.

In Reed's study (1958) of dog carcass communities he identified four stages of decomposition. These stages, as determined in our study, and the characteristics of each are shown in Table 6. The chicken legs were still fresh on the third day of each cycle. On the fifth day the carrion was not completely bloated so it was designated as fresh-bloated. On the seventh day the carrion was clearly bloated. On the tenth day it was in the decay stage and in the dry stage on the twelfth and fourteenth days.

SUCCESSION IN THREE DISTINCT SHRUB AREAS. The general similarity of the three shrub areas with respect to the presence and abundance of carrion beetles is evident in Table 2. Silpha noveboracensis manifested a primary peak on the fifth day and a secondary peak on the tenth day in the Maple-leaved

Table 6. Characteristics of carrion (chicken leg) during two-week periods of decomposition in the summer of 1963.

	3rd Day	5th Day	7th Day	10th Day	12th Day	14th Day
Color	Clear	Darker	Black	Black	Black	Black
Odor	Slight	Moderate	Strong	Slight	Slight	Slight
Consistency	Firm	Firm	Mushy	Moist	Dry	Dry
Maggots	Few	Many	Many	Few	None	None
	(small)		-	(large)		
	FRESH	FRESH- BLOATED	BLOATED	DECAY	DRY	DRY

TABLE 7. Chi Square data for Maple-leaved Viburnum shrub area.

	Expected	Observed	X^2
3rd Day	12.3	24	$(24 - 12.3)^2 = 11.1$
5th Day	26.0	45	$\frac{12.3}{(45-26)^2} = 13.8$
7th Day	16.0	21	$\frac{26}{(21-16)^2} = 1.6$
10th Day	61.0	26	$\frac{16}{(26-61)^2} = 20.1$
12th Day	23.7	6	$\frac{61}{(6-23.7)^2} = 13.2$
14th Day	6.7	1	$\frac{(1 - 6.7)^2}{(1 - 6.7)^2} = 4.8$
			6.7
d.f. = 6	-1 = 5		$X^2 = 64.6$

Viburnum area. In the Arrowwood-Greenbrier and Black-haw areas a very high peak was present on the fifth day.

Nicrophorus sp. shows a plateau on days three to seven in Area 1. In Areas 2 and 3 a modest peak is evident on the tenth day. Silpha americana does not show a uniform pattern in this study. Prionochaeta opaca was present in low numbers in all three areas; however, no clear pattern was discernible.

Although it was apparent that there was general similarity in presence and abundance of carrion beetles in the three shrub areas, and it was also apparent that the numbers of *Silpha noveboracensis* and *Nicrophorus* sp. approximated the numbers for the same species in 1961 and 1963 (Tables 1 and 3) during early summer, careful observation seemed to indicate that the numbers of *Silpha noveboracensis* in the Maple-leaved Viburnum area might be somewhat different than the same species numbers in the other two areas. There was no question that *Silpha noveboracensis* was clearly the dominant species in all three shrub areas. However, the question remained, was there a significant difference in abundance of this species in the three shrub areas? The Chi Square statistic was used to help make this determination. The expected figure for each collecting day was the mean number of *Silpha noveboracensis* trapped in the three shrub areas. The observed figure was the number collected in the Maple-leaved Viburnum area.

Null hypothesis: There is no effect of shrub type on the abundance of Silpha noveboracensis.

Since the derived Chi Square of 64.6 (Table 7) is much greater than the theoretical Chi Square of 12.83, with 5 degrees of freedom, we must reject the null hypothesis and we must conclude, at the .05 level of significance, that the Maple-leaved Viburnum shrub area, in some manner, affected the abundance of *Silpha noveboracensis* differently than did the other two shrub areas tested

The temperature and rainfall observations were very similar in all three shrub areas. No rainfall was recorded in any of the three areas on any of the six collecting days and the temperature differences were very slight. On the third day of the cycle there was but one degree Fahrenheit difference in one of the areas. On days five, seven and 12 there was a range of two degrees and on days ten and 14 there was a spread of three degrees.

DISCUSSION

It would seem that the seven species of Silphidae found in Hutcheson Memorial Forest form a representative group of this family which are found in a large region of the U.S. roughly east of the Dakotas to the eastern seaboard and north of Georgia and Alabama to Canada. Payne and Crossley (1966) collected the same species near Clemson, South Carolina. Howden (1950) collected all but *Nicrophorus orbicollis* and *N. pustulatus* in North Carolina. Between Walker (1957) and Reed (1958) all seven species were recorded in Tennessee. All but *Silpha noveboracensis* and *Nicrophorus pustulatus* were recorded at Cedar Point, Ohio by Jaques (1915). Hatch (1927) recorded all but *Silpha inaequalis* for the State of Minnesota but he states that it may also be present in the State. Milne and Milne (1944) recorded all seven species as far north as Irondale, Ontario.

succession. I was surprised to find that there was very little succession within any given two-week cycle. The species that were present were usually present during most of the two weeks although it was true that the populations would build up and then drop off (Tables 1 and 3). Carrion seemed to be most attractive to carrion beetles from the fifth to the tenth days when it was in the fresh-bloated, bloated, and decay stages. Since this is the period of time during which the maggots were present (Table 6), it is possible that they are in some way involved in making the carrion habitat attractive to carrion beetles. It is probable that *Silpha* and *Nicrophorus* are predaceous on the maggots. Bell (1873), Clark (1895), Davis (1915), and Selous (1911) have reported observational evidence to this effect.

Although no succession was evident within any given cycle, there was on the other hand a very definite seasonal pattern of change in dominant populations of Silphidae through the six-week period of study. Whereas Silpha noveboracensis was the dominant species in early summer, it dropped off to a much lower level in early-middle summer and virtually disappeared in middle summer. Nicrophorus sp. was present in very small numbers in early summer but increased steadily during the summer. Its numbers rose above those of the former species during early-middle summer and increased sharply to make it the dominant species during middle summer when Silpha noveboracensis was all but gone (Table 5 and Fig. 2).

Since Nicrophorus sp. increased steadily as the former decreased, the high

numbers of individuals in family Silphidae were maintained so that this family persisted in being the dominant family in the carrion community during the six-week study period (Table 4 and Fig. 1). Families Staphylinidae and Histeridae are apparently predaceous on other insects on carrion (Arnett, 1963). Although the numbers depicting the presence and abundance of Staphylinidae rose and fell as did the numbers of Silphidae (Tables 1 and 3), the former were about one-half as abundant.

The disappearance of *Silpha noveboracensis* in middle summer was puzzling. Reed (1958) was apparently troubled by a similar experience. When speaking of the above species and of *Silpha inaequalis* he said, "This species, and the following species abruptly disappeared from the carcasses early in the season, a fact which I cannot explain." The last date which he gave was June 22. Howden (1950) likewise indicated that *Silpha noveboracensis* was not taken after June in her studies. As a result of these observations, along with my own findings, I am convinced that this species reproduces and terminates its activities relatively early during the summer.

To determine that the disappearance of *S. noveboracensis* was not a result of my collecting activities, I rechecked data obtained in 1964 and 1965. These data were taken from orientation studies (Shubeck, 1968) and were very important because few beetles were removed from the forest during the studies conducted these summers. It is true that the beetles that had been marked and recaptured were then destroyed but this was a relatively small portion of those present. It amounted to 50 individuals of *Silpha noveboracensis* in 1964 and 112 individuals of this species in 1965.

It was interesting to note that on several occasions, during the early summer and early-middle summer seasons, the tiny *Prionochaeta opaca* (Leptodiridae) increased in numbers as the other carrion beetles decreased. This usually occurred during the latter phase of decomposition when the carrion was in the dry stage. This was the one species that seemed to have a fixed position, when present, among the beetles present during carrion decomposition. Although members of this family are commonly referred to as the Small Carrion Beetles, many of its species feed on fungus (Arnett, 1963). It is possible that *Prionochaeta opaca* was feeding on fungus growing on the carrion.

Although Silphidae were usually present on most collecting days during decomposition of carrion, the greater numbers were taken on days five, seven and ten. The carrion was in the fresh-bloated, bloated, and decay stages on these days (Table 6). Reed (1958) found that Silphidae were frequently present in large numbers during the bloated and decay stages but in very small numbers during the fresh and dry stages of decomposition. Payne and Crossley (1966), on the other hand, found the Silphidae virtually limited to the decay stage.

SUCCESSION IN THREE DISTINCT SHRUB AREAS. The fact that the results were

basically the same in all three shrub areas seems to indicate that specific shrub areas, having similar microclimates, within a forest region have only a minor effect on the presence and abundance of carrion beetles. Walker (1957) attributed the differences that he noted in his study to different microclimates. The Silphidae that are present in a given forest region probably cruise through the area until they detect the odor of carrion and are able to locate it.

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